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Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae)

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Abstract. The scorpion *Apistobuthus susanae* Lourenço 1998 is redescribed based on new specimens collected from Khoozestan Province, Iran. It is distinct from *A. pterygocercus* Finnegan 1932 found in the dunes of Rub' al-Khali. The two species cannot be separated by previously used diagnostic characters. Instead, *A. susanae* is differentiated from *A. pterygocercus* by new characters, including more robust legs and pedipalps, shorter pectines, stronger carination, and complete fusion of central lateral and posterior median carinae of the carapace.

Keywords: Taxonomy, scorpion, Iran, Arabia

In 1932, Dr. Susan Finnegan at the British Museum of Natural History studied three specimens of a remarkable new buthid scorpion collected by the British explorer Sir Bertram Thomas in 1930, on his camel voyage across the vast sand sea of southern Arabia, the Rub' al-Khali or Empty Quarter (Thomas 1931, 1932). She assigned this scorpion to a new genus and species, *Apistobuthus pterygocercus* or "incredible buthid with winged tail," a reference to the laterally flared disc-shaped second metasomal segment, a feature unique among all known scorpions. The syntypes were all immatures, and not until 1960 did Vachon describe the morphology of an adult female collected by Wilfred Thesiger from Wadi Andhur in the Dhofar Province of Oman during one of his own camel treks across Arabia (Thesiger 1959). Additional records of the species have been published by Vachon (1979) and Hendrixson (2006) from Saudi Arabia, and Al Safadi (1992) from Yemen, all associated with sand systems in the central and southern regions of the Arabian Peninsula.

The genus *Apistobuthus* remained monotypic until Lourenço (1998) described a second species, *A. susanae*, from Ahvaz in the Khoozestan Province of Iran. The new species was distinguished from *A. pterygocercus* using four characters: trichobothrial pattern, dentition of the anal arc, pectinal tooth counts, and number of subrows of denticles on the pedipalp fingers. However, these characters are known to exhibit variation within scorpion populations, and since the species diagnosis was based on a single type specimen, the validity of this species needs to be confirmed. We recently collected a large series of *Apistobuthus* from several localities in Khoozestan Province (Navidpour et al. 2008) that bracket the type locality (Ahvaz) of *A. susanae*. Analysis of this material reveals that *A. susanae* is indeed distinct from *A. pterygocercus*, but new characters are required to differentiate the two species.

METHODS

Study specimens of *Apistobuthus susanae* and *A. pterygocercus* were collected in the field by means of ultraviolet light detection, or loaned by museums. Examination of cuticular morphology and photomacrography was facilitated by ultraviolet (UV) fluorescence imaging (Prendini 2003a, 2003b, 2004; Volschenk 2005) using an LED excitation source (Lowe et al. 2003). All anatomical photographs in the figures were taken with UV epifluorescence except for Fig. 17, which was taken with transmitted oblique illumination. Measurements were made with digital calipers or an eyepiece reticle, and generally followed the conventions of Lamoral (1979) and Sissom et al. (1990), with the following exceptions: carapace anterior width taken between most medial pair of lateral eyes; telson and vesicle lengths taken from anterior limit of vesicle, pedipalp chela length taken as chord length from external proximal end of manus to finger tips; pedipalp manus width and depth taken with articular condyles level; and metasoma III width excluding enlarged lateral spiniform granules. Carinal terminology follows Stahnke (1970), except that we follow the amendments to nomenclature of metasomal carinae introduced by Prendini (2001b, 2004). Trichobothrial terminology follows Vachon (1974, 1975), and hemispermatophore terminology follows Lamoral (1979). Statistics of samples are expressed as mean ± standard deviation (SD).

Abbreviations.—*Specimen depositories*: MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum, Basel, Switzerland; ONHM, Oman Natural History Museum, Muscat, Oman; RRLS, Razi Reference Laboratory of Scorpion Research, Ahvaz, Khoozestan, Iran; TERC, Terrestrial Environment Research Centre, Environment Agency, Abu Dhabi, United Arab Emirates; ZMUH, Zoologische Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany. *Private collections*: EV, Erich Volschenk, Western Australian Museum, Perth; FKCP, František Kovařík, Prague, Czech Republic; GL, Graeme Lowe, Philadelphia, Pennsylvania; MES, Michael E. Soleglad, Borrego Springs, California; VF, Victor Fet, Marshall University, West Virginia. *Biometrics*: L, length; W, width; D, depth.

Comparative material examined.—*Apistobuthus pterygocercus*: OMAN: 1 ♀, ca. 57 km S of Hafit, 23°29′N, 55°52′E, 200 m, 31 March 1994, M.D. Gallagher, B.J. Tigar MDG 8592 (NMB); 1 ♂, Ramlat Muqshin, 19°30.86′N, 54°36.71′E, 195 m, 6 October 1994, G. Lowe, M.D. Gallagher (ONHM); 1 ♂, 1 ♀, NW of Montesar, S of Wadi Muqshin, 19°29.17′N, 54°36.89′E, 200 m, 6 October 1994, G. Lowe, M.D. Gallagher (NMB); 2 ♀, Ramlat As Sahmah, 20°13.87′N, 55°54.75′E,

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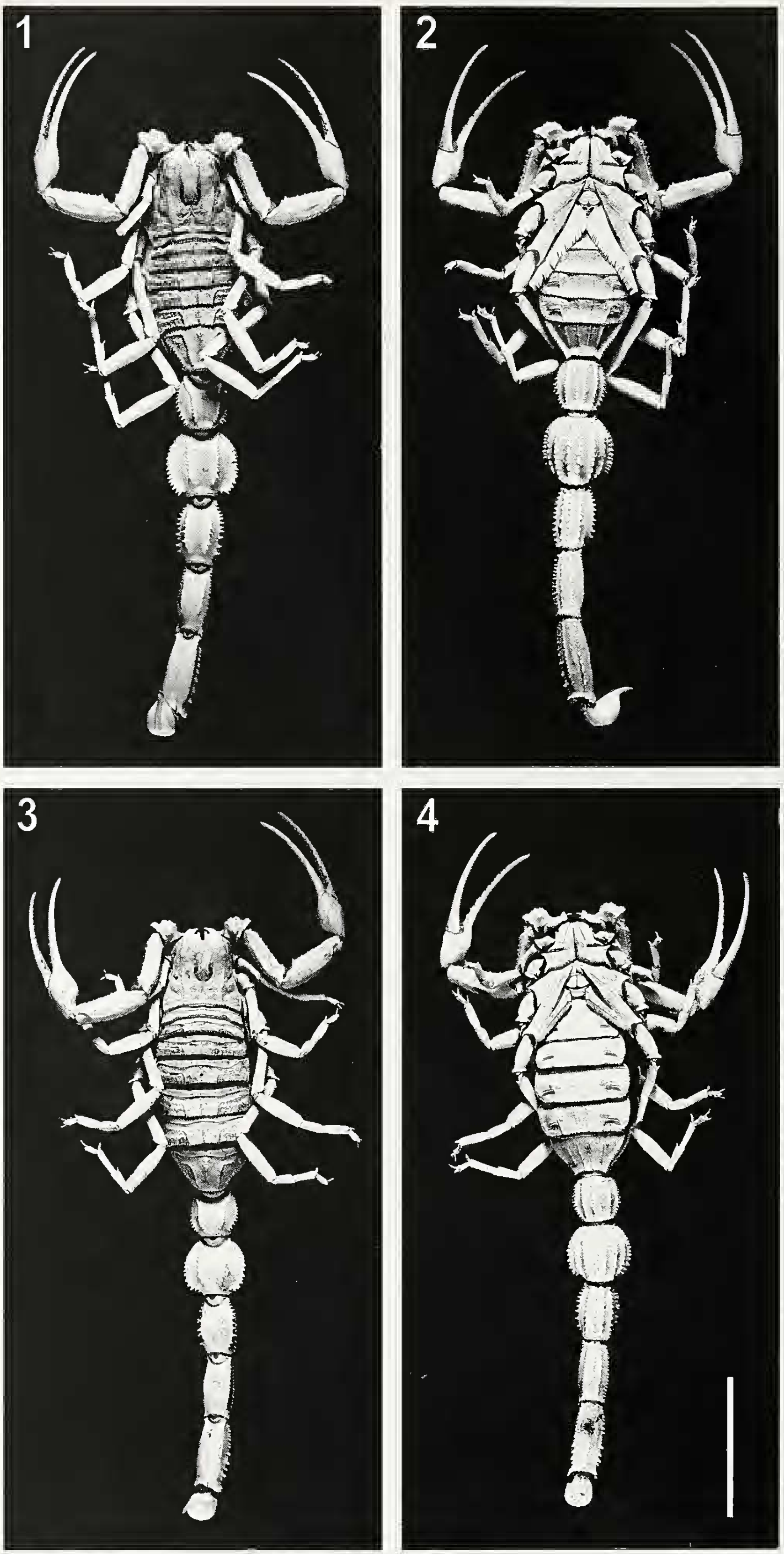
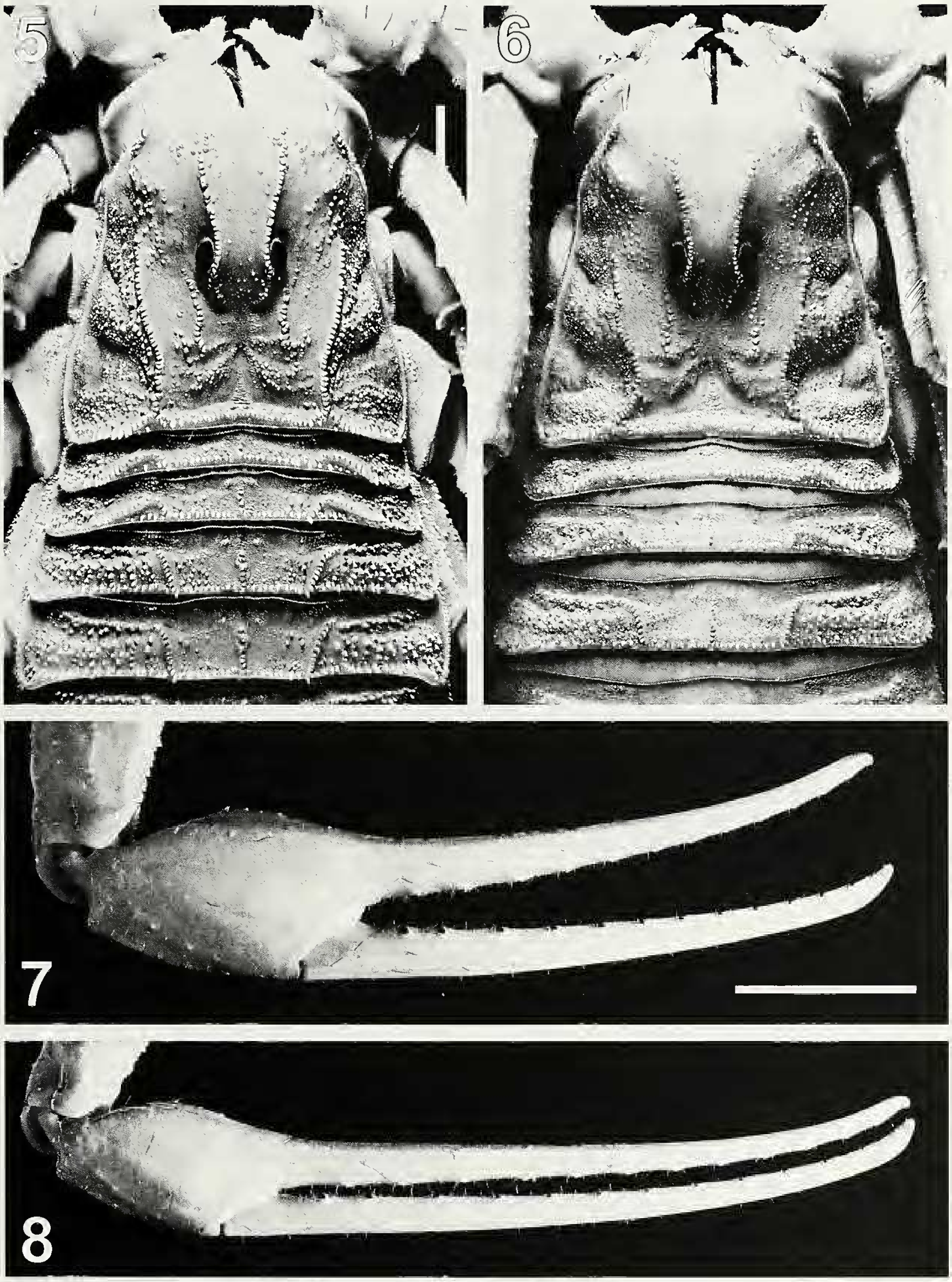
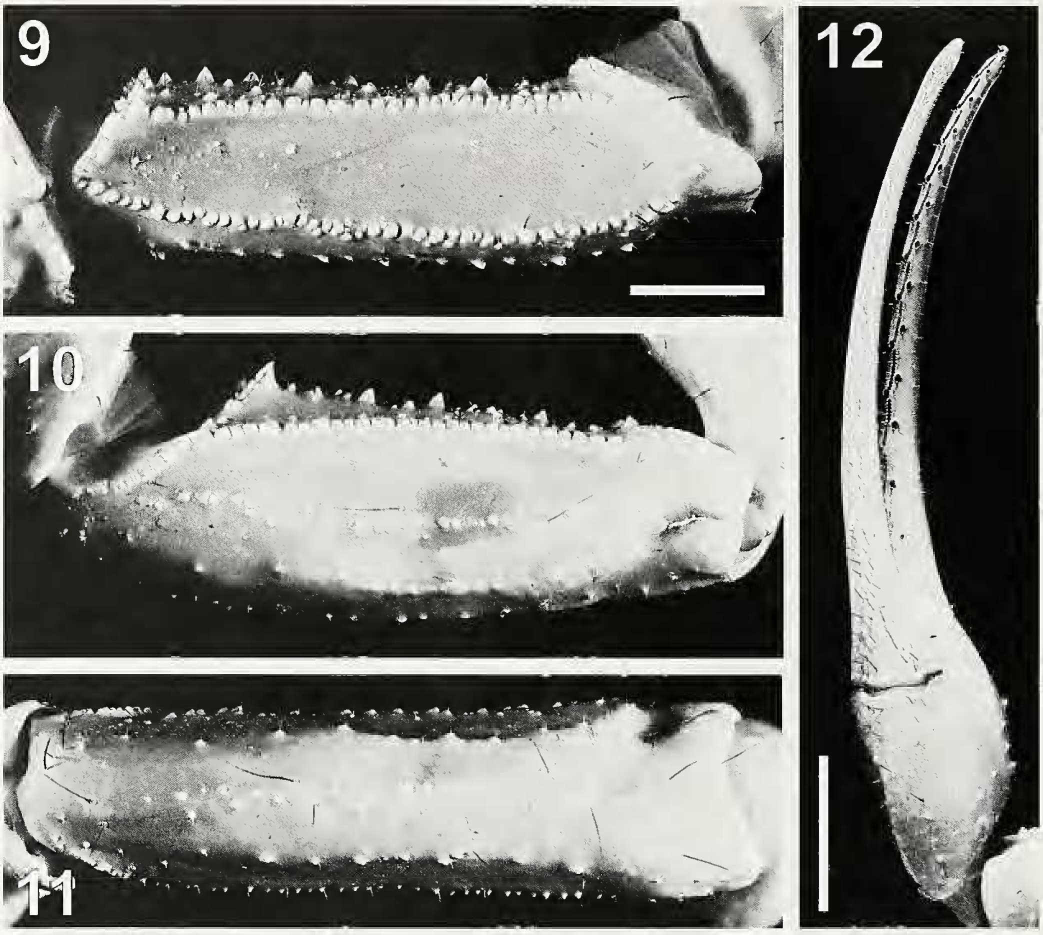


Figures 1–4.—*Apistobuthus susanae*, habitus. 1, 2 . Adult male from Bostan; 1. Dorsal aspect; 2. Ventral aspect; 3, 4. Adult female from Omidiyeh; 3. Dorsal aspect; 4. Ventral aspect. Scale bar = 20 mm.



Figures 5–8.—*Apistobuthus susanae*, adult male from Bostan, and *A. pterygocercus*, adult male from Uruq Al Hadd. 5, 6. Carapace and anterior tergites; 5. *A. susanae*; 6. *A. pterygocercus*; 7, 8. External aspect of pedipalp chela; 7. *A. susanae*; 8. *A. pterygocercus*. Vertical scale bar = 5 mm in 5, 4.87 mm in 6; horizontal scale bar = 5 mm in 7, 5.56 mm in 8.

165 m, 7 October 1994, G. Lowe, M.D. Gallagher (FKCP); 1 ♂, 1 ♀, Ramlat As Sahmah, 20°11.66′N, 55°57.41′E, 170 m, 7 October 1994, G. Lowe, M.D. Gallagher (NMB); 1 ♂, Ramlat Fasad, 18°32.44′N, 53°05.06′E, 240 m, May 1995, A. Dunsire (FKCP); 1 ♂, Wadi Atiyah, 18°17.09′N, 53°14.45′E, 260 m, 28 September 1995, G. Lowe, M.D. Gallagher, A. Dunsire (FKCP); 1 ♀, 55 km NW Ibri, 23°36.5′N, 56°05.33′E, 290 m, 22 November 1995, J. Dundon (GL); 1 ♀, Rub' al-Khali, Margandid, Montesar area, 19°36.85′N, 54°18.68′E, 1.XII.1995, J. Everett; 3 ♂, 1 ♀, Uruq al Hadd, Rub'Al Khali, 224 km WNW Thumrait, 18°53.6′N, 52°20.32′E, 11 January 1996, J.N. Barnes (EV, GL); 1 ♀, between Qarn Alan & Ghabah North, 21°22.03′N, 57°05.47′E, 150 m, 21 February 1996, M.D. Gallagher, MDG 8755 (NMB); 1 ♂, 1 ♀, 15 km NW of Shigag, 19°37.4′N, 54°04′E, 190 m, 30 November 1997, M.D. Gallagher & I.D. Harrison MDG 8909 (GL); 2 ♂, 15 km NNE. Fasad, 18°45.2′N, 53°08.9′E, 290 m, 29 January 1998, M.D. Gallagher, J.N. Barnes, MDG 8940 (ONHM). QATAR: 'Doha' (Ad Dawhah), 25°15″N, 51°34′E, 22 March 1963, A.J. Warr (MNHN RS4065). UNITED ARAB EMIRATES: 1 ♂, Zaid,



Figures 9–12.—*Apistobuthus susanae*, pedipalp, adult male from Bostan. 9. Pedipalp femur, dorsal aspect. 10. Pedipalp patella, dorsal aspect. 11. Pedipalp patella, external aspect. 12. Pedipalp chela, ventral aspect. Horizontal scale bar = 2 mm in 9, 2.15 mm in 10–11, vertical scale bar = 4 mm in 12.

dunes of Bada, Abu Dhabi, 9 July 1971, D.J.G. Williams (MNHN RS6509); 1 ♂, Bada Zaid, Abu Dhabi, dunes, March? 1972, D.J.G. Williams (MNHN RS6486); 1 ♀, Zaaba, camp area, dunes, 23°42.45′N, 55°29.33′E, June 1972, D.J.G. Williams (MNHN RS6940); 1 ♂, Zaaba, camp area, 23°42.45′N, 55°29.33′E, 12 July 1972?, D.J.G. Williams (MNHN RS6488); 2 ♀, Zaaba, camp area, 23°42.45′N, 55°29.33′E, 14 July 1972, D.J.G. Williams (MNHN RS6489, RS6942); 1 ♂, Khawr Fakhan, 25°20.47′N, 56°21.03′E, August 1972 (MNHN RS6490); 1 ♀, Dubai, 25°10.8′N, 55°15.6′E, September 1972, M.D. Gallagher, MDG 2185, (MNHN RS6485); 1 ♂, Juweiza, 25°20′N, 55°40′E, 8 March 1973, M.D. Gallagher MDG 2312 (MNHN RS6919); 1 ♂, Sweihan, 24°27.97′N, 55°19.88′E, 30 October 1993, (TERC).

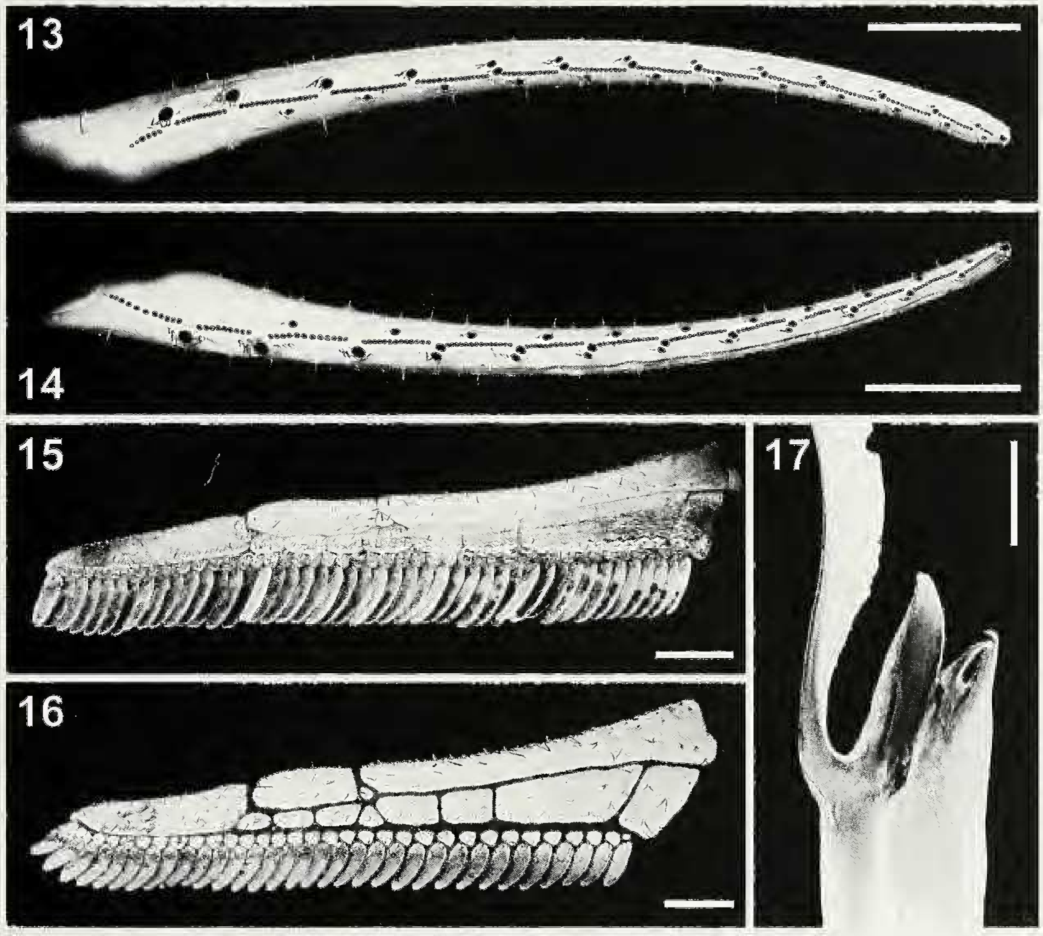
SYSTEMATICS

Family Buthidae C.L. Koch 1837
Apistobuthus Finnegan 1932

Apistobuthus Finnegan 1932:92.

Type species.—*Apistobuthus pterygocercus* Finnegan 1932

Diagnosis.—Medium to large buthids (Sissom 1990), adults 80–100 mm in length, carapace and tergites granulated; carapace with well developed anterior, superciliary, central median, central lateral, and posterior median carinae; posterior lateral carinae absent; anterior ocular region of carapace elevated relative to postocular region; tergites I–VI tricarinate, I–II with lateral carinae in a V-shaped configuration with two posteriorly directed arms; tergite VII with 5 carinae; metasoma elongate with segment II laterally dilated, disc-like; metasoma I with 10 denticulate carinae; metasoma II with 10 carinae, dorsosubmedian carinae denticulate, dorsolateral carinae strongly flared laterally, crenulate; median lateral, ventrolateral and ventromedian carinae smooth to vesiculate-granulate; metasoma III with 8 carinae bearing enlarged spiniform granules; metasoma IV with 8 moderately spinose carinae; metasoma V with 3 dentate carinae (ventromedian and paired ventrolateral); telson with bulbous vesicle lacking subaculear spine or tubercle, aculeus long, curved; pectines with fulcra; cheliceral fixed finger armed with two denticles on ventral surface; pedipalps orthobothriotaxic, type Aβ (Vachon 1974, 1975); chela smooth with carinae reduced or obsolete, fingers elongated, movable finger > 2.6 times chela manus ventral length; pedipalp fingers armed with linear subrows of primary denticles (normally 13 on fixed, 14 on movable), more distal subrows with proximal enlarged denticle; subrows flanked by internal and external accessory denticles; movable finger with two enlarged subdistal internal denticles; males without scalloping at base of pedipalp fingers; tibial spurs present or absent on legs III–IV; basitarsi I–III



Figures 13–17.—*Apistobuthus susanae*. 13, 14. Pedipalp chela dentition, adult male from Bostan; 13. Movable finger; 14. Fixed finger; 15. Right pectine, adult male from Albaji; 16. Right pectine, adult female from Omidiyeh; 17. Basal lobes of right hemispermatophore, dorsal aspect, compressed to separate lobes; adult male from Omidiyeh. Scale bars = 2.5 mm in 13–15, 1 mm in 16, 500 µm in 17.

with bristle-combs; telotarsi ventrally smooth, lacking mid-ventral spines or setae; all legs with prolateral and retrolateral pedal spurs.

Comparisons: The buthid genera *Buthus*, *Leiurus* and *Odontobuthus* share the following characters with *Apistobuthus*: ventrolateral carinae of metasoma V with enlarged dentition; telson bulbous without subaculear tubercle, tibial spurs developed on legs III–IV (variable in *A. pterygocercus*), chelicera with two denticles on ventral aspect of fixed finger, pedipalps orthobothriotaxic type Aβ, carapace with central lateral and posterior median carinae partially or completely fused in a lyre configuration. Additionally, both *Odontobuthus* and *Apistobuthus* have strongly modified ventromedian carinae on metasoma II–III, and *Odontobuthus*, *Leiurus* and *Apistobuthus* have lateral carinae on tergites I–II that are either V-shaped, or split into a pair of carinae (in the case of *Leiurus*). *Apistobuthus* differs from these genera in several presumably autapomorphic characters, including the modified form and carination of metasoma II–III, highly elongated pedipalps, higher range of pectinal tooth counts, and elevated anterior ocular region of the carapace.

Apistobuthus susanae Lourenço 1998
Figs. 1–4, 5, 7, 9–27, Tables 1–2

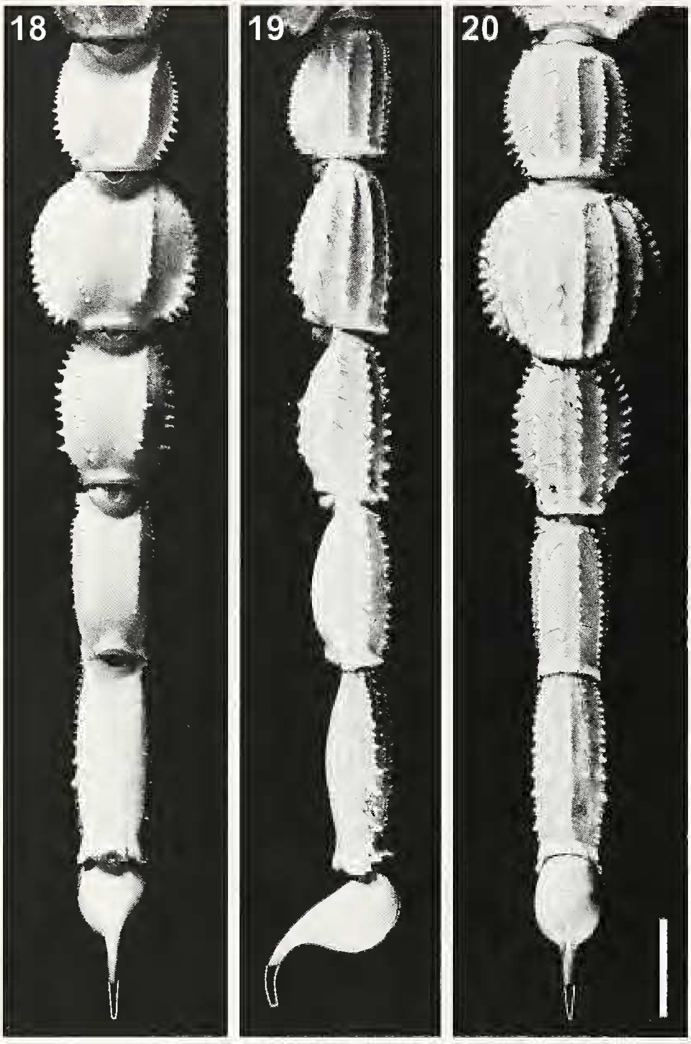
Apistobuthus sp.: Habibi 1971:45; Farzanpay 1988:36.

Apistobuthus susanae Lourenço 1998:238–244, figs. 8–14; Kovařík 1998:104; Fet & Lowe 2000:76; Navidpour et al. 2008:3–5, 7, 28, fig. 12.

Type specimen.—**Iran**: adult male, Ahvaz, summer 1961, T. Habibi (ZMUH A 27/98, not examined).

Material examined.—IRAN: *Khoozestan Province*: 2 ♂, 7 immature ♂, 3 immature ♀, Hamidiyeh, 31°27′57″N 48°29′18″E, 13 m, September 2007, Masihipour & Navidpour (NMB, RRLS, FKCP); 4 ♂, 3 immature ♂, 2 immature ♀, Bostan, 31°44′41″N 47°56′24″E, June 2007, Navidpour (NMB, VF, FKCP); 3 ♂, 3 ♀, 4 immature ♂, 4 immature ♀, Khoozestan Province, Omidiyeh, 30°57′49″N 49°31′47″E, Navidpour (NMB, RRLS, VF); 4 ♂, 4 ♀, Albaji, Ahvaz–Andimeshk road, 20 km to Ahvaz, 31°20′44″N 48°38′36″E, August 2005, Masihipour (NMB, GL, MES). KUWAIT: 1 ♀, "Koveit" (= Kuwait), D.A. Clayton (MNHN).

Diagnosis.—A species of *Apistobuthus* differentiated as follows: (1) pedipalp femur, patella and chela more robust than in *A. pterygocercus*, L/W ratios: femur 3.3–4.0 (n = 22), patella 2.5–3.3 (n = 22), chela 5.1–6.2 (n = 21) (Figs. 7, 9–12); pedipalp chela more inflated than in *A. pterygocercus*: manus W/carapace L 0.33–0.40 (n = 22); pedipalp fingers shorter: movable finger L/ carapace L 1.45–1.70 (n = 22), movable finger L/ chela manus ventral L 2.62–3.12 (n = 20); dentate margins of chela fingers usually bearing fewer primary



Figures 18–20.—*Apistobuthus susanae*, metasoma, adult male from Albaji. 18. Dorsal aspect; 19. Right lateral aspect; 20. Ventral aspect. Scale bar = 5 mm.

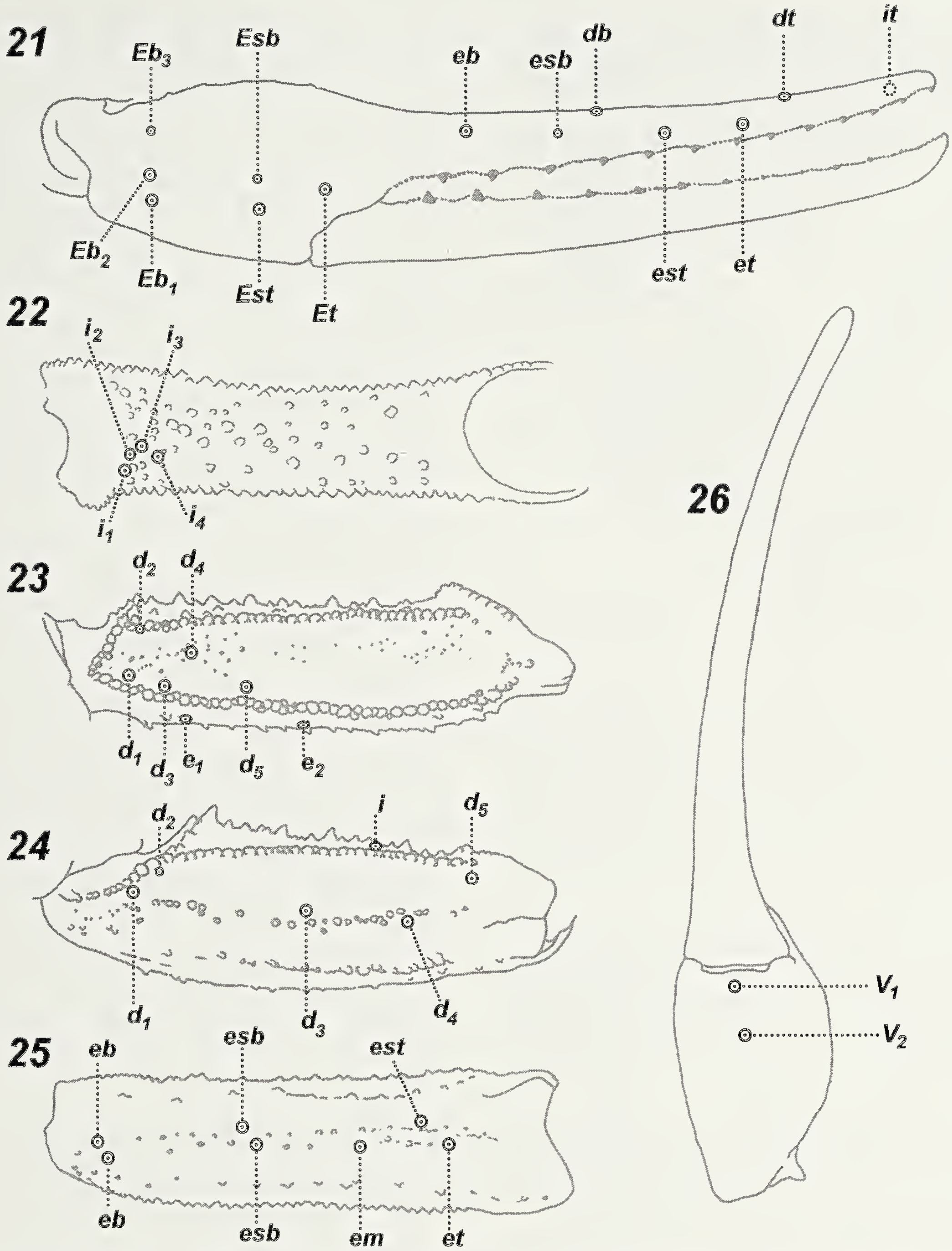
denticles than in *A. pterygocercus* (Figs. 13, 14); (2) pectines shorter than in *A. pterygocercus*, distal tips of pectines not extending past distal ends of coxa IV in females, and distal ends of trochanter IV in males; pectine teeth: males 42–48 (n = 41 combs), females 29–35 (n = 48 combs); (3) caparace and tergites with coarser granules and stronger carination than in *A. pterygocercus*; central lateral carinae of carapace strongly developed, fused with posterior median carinae to form a single continuous keel with gently curved lyre configuration (Fig. 5); (4) leg segments more robust than in *A. pterygocercus*: leg III patella L/D 3.1–3.8 (n = 21), ungues relatively short and stout; (5) metasoma II not as strongly flared as in *A. pterygocercus*: metasoma II W/ metasoma I W 1.35 ± 0.04, 1.29–1.41 (n = 21); with posterior enlargements of ventral carinae not overlapping metasoma III (Figs. 18–20).

In comparison, *A. pterygocercus* (Figs. 6, 8, 30–44, 46) differs as follows: (1) more slender pedipalps (Fig. 8): L/W ratios: femur 4.0–5.1, patella 3.4–4.5, chela 7.1–9.3 (n = 31) (Figs. 8, 34–36, 39); less inflated pedipalp chela: manus W/ carapace L 0.26–0.31 (n = 31); pedipalp fingers longer: movable finger L/ carapace L 1.69–2.08, movable finger L/ chela manus ventral L 3.64–4.63 (n = 31); fingers usually bearing higher numbers of primary denticles (Figs. 40, 41); (2) pectines extending up to or beyond distal ends of coxa IV (females) or trochanter IV (males); higher pectine tooth counts: males 49–59 (n = 34 combs), females 32–43 (n = 26 combs); (3) more moderately developed carination and finer granulation on the carapace and tergites; central lateral carinae of carapace weaker, may be partially broken, and often not fully fused and continuous with posterior median carinae; conjunction of central lateral and posterior median carinae forming a strongly curved lyre configuration (Fig. 6); (4) legs longer, more slender: leg III patella L/D 3.8.–4.4 (n = 13); tarsi with longer, more slender ungues (Fig. 46); (5) metasoma II with stronger lateral expansion: metasoma II W/ metasoma I W 1.47 ± 0.06, 1.36–1.61 (n = 31); ventral carinae of metasoma II more enlarged posteriorly, produced into angular protrusions overlapping anterior ventral margin of metasoma III (Figs. 42–44).

Morphometric differences between the two species for both sexes are summarized in Table 1. Comparative material representing *A. pterygocercus* that we analyzed was collected from a wide region spanning the southern margins of the Rub' al-Khali dunes, ranging from sites close to the two type localities along Thomas' route (Uruq adh Dhahiqah, Shena), across central Oman to Abu Dhabi in the United Arab Emirates (Fig. 27).

Etymology.—The species was named after Dr. Susan Finnegan who, as noted by Lourenço (1998), is the only female arachnologist to have described a new genus of scorpion. Dr. Finnegan also holds the distinction of being the first woman appointed to a post at the Natural History Museum in London. She succeeded Arthur Stanley Hirst in September 1927 as head of the Arachnida and Myriopoda Section, serving until her retirement in July 1936. Another scorpion, *Hottentotta finneganae* Kovařík 2007, was also named in her honor.

Redescription.—*Coloration*: entire body light yellow or light tan; carapace sometimes with variable dusky markings around median ocular tubercle, interocular triangle and carinae; ocular tubercle dark; telson aculeus and denticles of chelicerae and pedipalp fingers black. *Carapace* (Fig. 5): subrectangular, anterior W/posterior W 0.48–0.55 (n = 21); anterior half of carapace including median ocular tubercle elevated relative to posterior half; ocular tubercle broad, prominent, distance from anterior margin 0.43–0.48 times carapace length; anterior and superciliary carinae continuous, strong, granulose; anterior margin of carapace straight, rimmed with row of coarse granules, with < 10 macrosetae; linear array of 3–5 lateral eyes on each side, bordered with row of granules; central median carinae moderate, granulose; central lateral and posterior median carinae strong, granulose, fused into continuous keel; posterior margin of carapace rimmed with continuous row of granules, joined to posterior median carinae; lateral flanks of carapace steeply sloped; intercarinal areas studded with varying coarse to fine granulation. *Chelicera*: robust, manus with dorsal surface smooth proximally, with scattered granules distally, dorsointernal carina at base of fixed finger granular; ventral surface of manus smooth with sparse setation centrally, dense brush of setae on medial apical aspect and base of fixed finger; dentition following typical buthid pattern: fixed finger with large distal tine,



Figures 21–26.—*Apistobuthus susanae*, adult male from Bostan, map of trichobothrial pattern of right pedipalp. 21. Chela, external aspect; 22. Femur, internal aspect; 23. Femur, dorsal aspect; 24. Patella, dorsal aspect; 25. Patella, external aspect; 26. Chela, ventral aspect.

moderate subdistal denticle and large proximal bicusp on dentate margin, two prominent denticles on ventral aspect; movable finger with large dorsal distal tine, and shorter downward deflected ventral distal tine; dorsal margin of movable finger with two subdistal denticles and two small contiguous proximal denticles; ventral margin with two robust subdistal denticles. *Coxosternal area* (Figs. 2, 4): all coxae finely granular or shagreened; coxae II–III with granular anterior carinae; coxa IV with granular or crenulate anterior and posterior carinae; sternum triangular, coarsely granular, with deep median longitudinal sulcus; genital opercula granular on lateral surfaces, smooth medially. *Pectines* (Figs. 15, 16): basal piece with fine to coarse granulation medially, smooth laterally; distal tips of pectines not extending past distal ends of coxa IV in females, not past distal ends of trochanter IV in males; pectines with 3 marginal lamellae, 7–9 middle lamellae; pectine teeth of males 44–48 (n = 22 combs, mode = 46 with 8 combs), females 29–33 (*n* = 20 combs, mode = 32 with 8 combs). *Mesosoma* (Figs. 1–5): pretergites smooth; tergites I–VI tricarinate, median and lateral carinae strong, granular; posterior margins armed with row of granules; tergites I–II with lateral carinae in a V-shaped

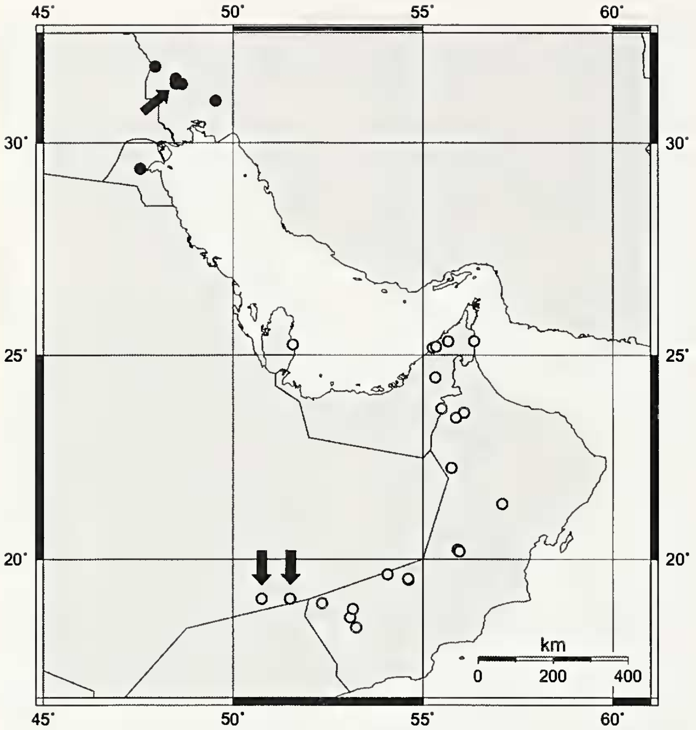


Figure 27.—Map of records for *Apistobuthus susanae* (closed circles) and *A. pterygocercus* (open circles). Coordinates of all material examined in this study are plotted, and also those for the holotype of *A. susanae* (diagonal arrow: Ahvaz, 31° 21.08′N, 48°38.3′E), and syntypes of *A. pterygocercus* (vertical arrows: Uruq adh Dhahiqah, Saudi Arabia, 19°00′N, 51°30′E; Shena, Saudi Arabia, 19°00′N, 50°45′E; coordinates from Thomas 1931). The record from Kuwait is plotted with approximate coordinates (29°24′N, 47°33′E).

configuration with two posteriorly directed arms; tergite VII with 5 carinae; medial intercarinal surfaces finely granular, lateral surfaces coarsely granular; tergite VII pentacarinate, all carinae strong, granular, medial intercarinal surfaces smooth, lateral surfaces sparsely granular; sternite III with 2 divergent carinae joined anteriorly; sternites IV–VII tetracarinate; all sternites shagreened or with dense, fine granulation; sternites IV–VI smooth behind spiracles; sternite VII smooth laterally; sternites III–VI with large slit-like spiracles; posterior and lateral margins of all sternites with row of fine granules or denticles. *Hemispermatophore* (Fig. 17): trunk long, slender; flagellum long, about equal in length to trunk when extended; inner lobe a broad blade, rounded apically; median lobe short, narrow; outer lobe short, tapered, apically flexed; basal lobe distinct, digitate; measurements (male from Omidiyeh): trunk L (to base of flagellum) 11.4 mm, pars recta 4.4 mm, inner lobe (from base of flagellum) 960 μm, median lobe 415 μm, outer lobe 360 μm, basal lobe 100 μm. *Metasoma* (Figs. 18–20): metasoma I with 10 denticulate carinae; metasoma II with 10 carinae, dorsosubmedian carinae denticulate, dorsolateral carinae strongly flared, crenulate to denticulate with enlarged serrate armature posteriorly; median lateral, ventrolateral and ventromedian carinae robust, thickly sclerotized, smooth to vesiculate-granulate; ventromedian carinae with posterior granules enlarged, tuberculiform, not projecting over metasoma III; metasoma III with 8 carinae, armed with enlarged, sharp conical denticles or spiniform granules; metasoma IV with 8 carinae; dorsosubmedian and dorsolateral carinae weak, with small dentate granules; ventrolateral and ventromedian carinae strong, denticulate; metasoma V with dorsolateral carinae smooth or obsolete, ventrolateral and unpaired ventromedian carinae strong, denticulate; ventrolateral carinae with larger posterior denticulations separated by finer denticulations; ventrosubmedian carinae weak, confined to anterior 2/3 of metasoma V, marked by broad strip of fine and coarse granules; metasoma I–III with all intercarinal surfaces smooth; metasoma IV–V with dorsal and lateral surfaces smooth, ventral surfaces finely shagreened. *Telson* (Figs. 18–20): vesicle bulbous, smooth, lacking subaculear spine or tubercle; aculeus long, curved. *Pedipalp femur* (Fig. 9): dorsoexternal, dorsointernal, and ventrointernal carinae strong with dentate granules; exterior median carinae weak to obsolete, marked by dispersed row of granules and scattered long macrosetae; ventroexternal carina obsolete,

Table 1.—Morphometric differences between *Apistobuthus susanae* and *A. pterygocercus*. Sample size for each range of values is given in brackets as number of individuals for morphometric ratios, and number of combs or fingers for pectine teeth and denticle counts, respectively. Sample sizes marked with an asterisk (*) indicate that published data for the holotype female of *A. susanae* was included in the parameter ranges. Denticle counts enumerate the non-enlarged primary denticles, and exclude cases of teratology, abnormal development, fusion or splitting of subrows that result in more or less than 13 subrows (fixed finger) or 14 subrows (movable finger). Data are from adults except for number of pectine teeth, which is independent of age.

	Males		Females	
	A. susanae	*A. pterygocercus*	*A. susanae*	*A. pterygocercus*
Pedipalp femur L/W	3.52–4.02 (11)	4.13–5.10 (18)	3.29–4.02 (11*)	4.01–4.83 (13)
Pedipalp patella L/W	2.92–3.27 (11)	3.61–4.49 (18)	2.58–3.23 (11*)	3.40–4.00 (13)
Pedipalp chela L/manus W	5.54–6.19 (11)	7.61–9.25 (18)	5.06–6.00 (10*)	7.17–8.09 (13)
Pedipalp movable finger L/chela manus ventral L	2.62–3.01 (11)	3.64–4.33 (18)	2.76–3.12 (9)	3.78–4.63 (13)
Pedipalp movable finger L/manus W	4.28–4.86 (11)	6.10–7.75 (18)	3.89–4.67 (11*)	5.77–6.73 (13)
Pedipalp chela manus ventral L/manus W	1.48–1.70 (11)	1.56–1.80 (18)	1.39–1.60 (9)	1.25–1.65 (13)
Pedipalp movable finger L/carapace L	1.55–1.62 (11)	1.69–2.08 (18)	1.45–1.70 (11*)	1.75–2.02 (13)
Pedipalp manus W/carapace L	0.33–0.38 (11)	0.26–0.31 (18)	0.35–0.40 (11*)	0.29–0.31 (13)
Leg III patella L/W	3.44–3.80 (11)	4.03–4.37 (6)	3.16–3.73 (9)	3.82–4.17 (7)
Pectine teeth	42–48 (41)	49–59 (34)	29–35 (48*)	32–43 (26)
Fixed finger primary denticles	143–166 (16)	156–198 (29)	142–163 (17)	164–202 (23)
Movable finger primary denticles	155–172 (18)	164–203 (31)	146–166 (16)	166–207 (22)

Table 2.—*Apistobuthus susanae*, measurements of representative adult male and female (lengths in mm).

	Male, Bostan	Female, Omidiyeh
Total L	88.00	91.00
Metasoma + Telson L	58.30	56.00
Carapace L/ anterior W/ posterior W	10.43/ 5.83 /10.82	10.70/ 6.29/ 12.73
Median ocular tubercle to anterior margin	4.73	4.72
Metasoma I L/ W/ D	7.37/ 7.67/ 5.66	7.31/ 7.61/ 5.63
Metasoma II L/ W/ D	9.07/ 10.36/ 5.77	9.50/ 9.83/ 5.57
Metasoma III L/ W/ D	9.20/ 5.81/ 5.08	9.69/ 6.40/ 5.30
Metasoma IV L/ W/ D	9.81/ 4.57/ 4.25	9.18/ 5.17/ 4.88
Metasoma V L/ W/ D	12.00/ 4.70/ 3.67	11.60/ 5.04/ 4.08
Telson L	10.30	10.32
Vesicle L/ W/ D	5.71/ 4.36/ 3.75	5.91/ 4.44/ 4.27
Pedipalp chela L	21.66	21.61
Pedipalp chela chela manus ventral L	5.72	6.03
Pedipalp chela manus W/ D	3.52/ 4.23	4.02/ 4.59
Pedipalp chela fixed finger L/ movable finger L	14.63/ 16.92	14.38/ 16.67
Pedipalp femur L/ W	10.45/ 2.77	10.14/ 2.70
Pedipalp patella L/ W	11.66/ 3.68	11.62/ 3.68
Pectine L	13.32	9.01
Pectine teeth Left/Right	46/ 47	32/ 33
Ventral anal arc, denticles	8	8
Movable finger primary denticles, Left/ Right	160/ 163	160/ 161
Fixed finger primary denticles, Left/ Right	154/ 153	154/ 148
Leg III patella, L/ D	9.80/ 2.58	9.63/ 2.75

marked on distal half by row of short macrosetae; dorsal surface of femur smooth except for scattered small granules on proximal area, ventral surface smooth except for proximal cluster of granules, internal surface studded with large conical granules interspersed with small granules. *Pedipalp patella* (Figs. 10, 11): dorsointernal, ventrointernal, and ventromedian carinae strong, with dentate granules; internal surface with dorsal patellar spur carinae bearing enlarged dentate granules interspersed with smaller dentate granules, and several long macrosetae; ventroexternal carina weak with sparse low granules; exterior median carina moderate with irregular granules; dorsomedian and dorsoexternal carinae weak to moderate with irregular small to large granules; intercarinal surfaces of patella mostly smooth, only lightly shagreened in small areas. *Pedipalp chela* (Figs. 7, 12): smooth; dorsomarginal, digital, and external secondary carinae weak, smooth; ventroexternal carinae weak to moderate, smooth; manus slightly inflated, fingers long and tenuous; fixed finger normally with 13 subrows of primary denticles, movable finger normally with 14 subrows; proximal enlarged primary denticle normally absent on proximal 4 subrows of fixed finger, proximal 5 subrows of movable finger; denticle subrows on fingers flanked by enlarged external accessory denticle, sometimes reduced or absent on distal 1–2 subrows; all denticle subrows flanked by internal accessory denticle, ventral surface of manus with up to a dozen moderate length macrosetae; ventral surface of movable finger with abundant short, fine macrosetae. *Trichobothrial pattern*: orthobothriotaxic type Aβ, with full complement of normal and petite trichobothria (Figs. 21–26); femur with d_2 on dorsal surface, patella with d_3 internal to dorsomedian carina, chela fixed finger with *esb* and *eb* situated between *db* and *dt*. *Legs*: moderately slender, segments with granular carinae; femur I–III, patella I–III and femur IV with strongly denticulate ventral carinae; tibia I —III and basitarsi I —III with prominent bristle-combs on retrolateral margins, and many long macrosetae on prolateral margins; prolateral and retrolateral pedal spurs setose, not bifurcated (Fig. 45). *Measurements*: data from representative male and female specimens are cited in Table 2.

Variation.—*Adults*: sexual dimorphism: males differ from females in having longer, pectines (pectine L/ carapace L, males 1.28–1.45, females 0.82–0.90), and longer pectine teeth that overlap basally; more robust carination and coarser granulation on carapace, tergites, and sternites; median carinae on sternites IV–V moderate, granular in males, weak to obsolete, smooth in females; in morphometrics, males as a group have slightly more slender pedipalps and legs, and a more elongated carapace (cited are means ± SD, n = sample size, U and $P < 0.05$ values from Mann–Whitney test): pedipalp femur L/W, male 3.80 ± 0.16 (11), female 3.65 ± 0.16 (10), $U = 24$, $P = 0.03$; chela L/W, male 5.91 ± 0.24 (11), female 5.52 ± 0.32 (9), $U = 16$, $P = 0.01$; pedipalp chela manus ventral L/manus W, male 1.62 ± 0.07 (11), female 1.48 ± 0.06 (9), $U = 9$, $P = 0.002$; chela manus W/D, male 0.84 ± 0.03 (11), female 0.87 ± 0.02 (10), $U = 20$, $P = 0.014$; chela movable finger L/manus W, male 4.60 ± 0.20 (11), female 4.33 ± 0.27 (10), $U = 25$, $P = 0.035$; leg III patella L/W, male 3.61 ± 0.10 (11), female 3.43 ± 0.16 (9), $U = 15$, $P = 0.009$; carapace L/W, male 0.92 ± 0.03 (11), female 0.89 ± 0.03 (10), $U = 24$, $P = 0.03$. *Morphometric ratios*: both sexes pooled (n = sample size): carapace L/W 0.84–0.96 (21), median ocular tubercle to anterior margin/ carapace length 0.43–0.48 (21), metasoma I L/W 0.91–1.05 (21), metasoma II L/W 0.82–0.97 (21), metasoma III L/W 1.23–1.66 (21), metasoma IV L/W 1.78–2.15 (21), metasoma V L/W 2.30–2.78 (21), pedipalp femur L/W 3.49–4.02 (21), pedipalp patella L/W 2.58–3.27 (21), pedipalp chela L/W 5.06–6.19 (20), pedipalp chela manus W/D 0.78–0.91 (21), pedipalp chela manus ventral L/chela W 1.39–1.70 (20), pedipalp movable finger L/chela manus ventral

Figures 28, 29.—Habitat of *Apistobuthus susanae*. 28. Site at Omidiyeh; 29. Site at Bostan.

L 2.62–3.12 (20), pedipalp fixed finger L/chela manus ventral L 2.22–2.70 (20), pedipalp chela manus W/carapace length 0.33–0.40 (21), pectine L/carapace L 0.82–1.45 (21), leg III patella L/W 3.16–3.80 (20), pedipalp movable finger L/carapace L 1.45–1.69 (21), pedipalp femur L/carapace L 0.90–1.06 (21), pedipalp patella L/carapace L 1.02–1.18 (21). *Juveniles*: similar to adults, but with less pronounced lateral expansion of metasoma II.

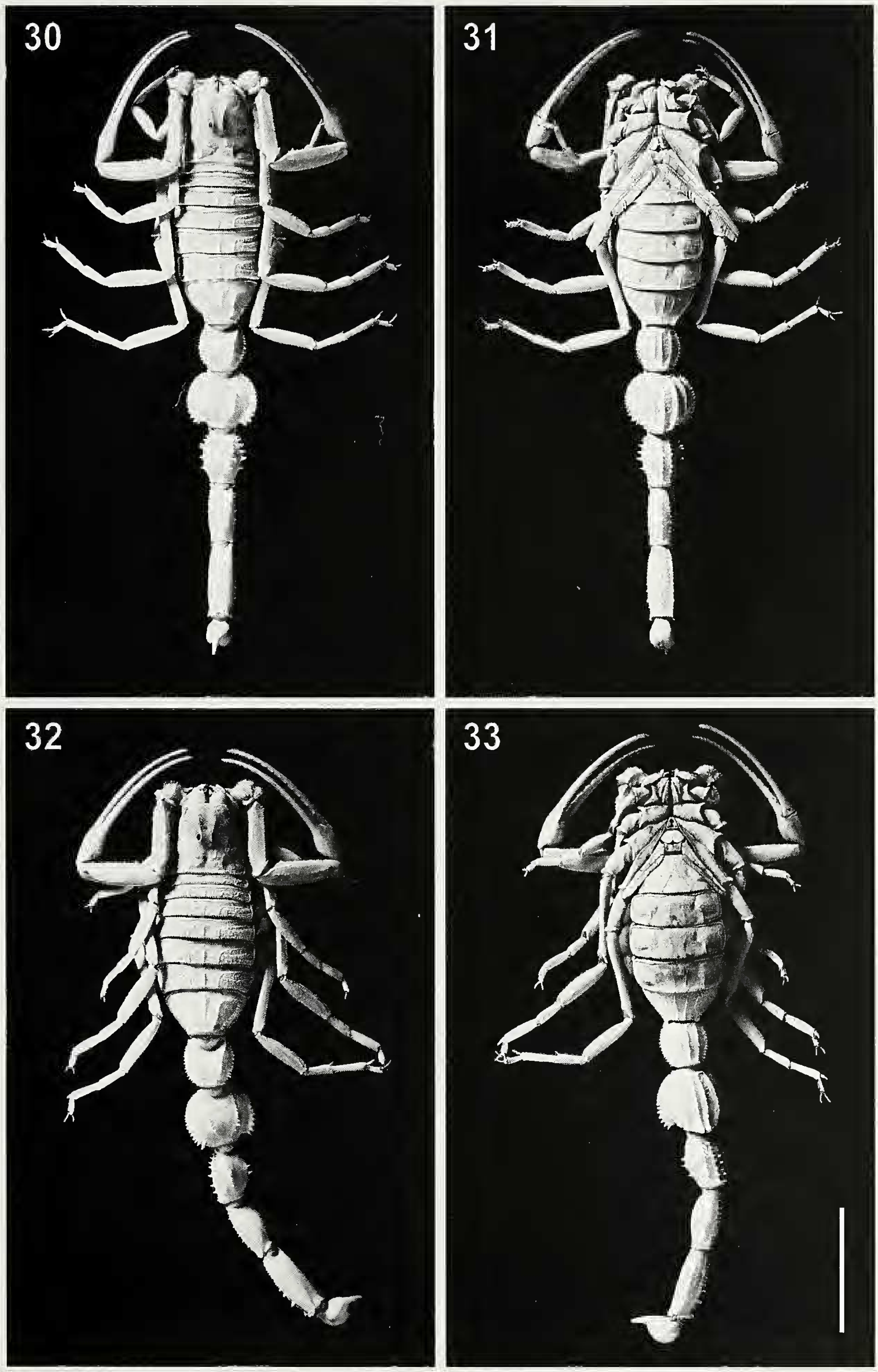
Although we have not examined the holotype female from Ahvaz, it is an adult (carapace L = 10.2 mm) and, based on the morphometric data provided by Lourenço (1998), it is clearly grouped with our sample from the region of Khoozestan Province surrounding Ahvaz, and is distinguishable from *A. pterygocercus*: pedipalp movable finger L/manus W 4.33, pedipalp femur L/W 3.29, pedipalp patella L/W 3.03, pedipalp chela L/W 5.85, pedipalp manus W/carapace L 0.39, pedipalp movable finger L/carapace L 1.70. In addition to the Khoozestan material, an adult female from Kuwait, previously loaned from MNHN and examined, is also assigned here to *A. susanae* on the basis of morphometric diagnostic characters: pectine teeth 33/32, pedipalp femur L/W 3.61, pedipalp patella L/W 2.73, pedipalp movable finger L/chela W 4.67, pedipalp chela W/carapace L 0.36, pedipalp movable finger L/carapace L 1.69.

The majority of our *Apistobuthus* material originates from sample sites that are widely separated geographically. However, one adult male that we analyzed was labeled "Doha, Qatar," which is situated roughly midway between Ahvaz and Uruq adh Dhahiqah, the type localities for the two species (Fig. 27, open circle). Morphometric data for this specimen is consistent with our series of *A. pterygocercus* from southern Rub' al Khali: pedipalp movable finger L/manus W 6.54, pedipalp femur L/W 4.32, pedipalp patella L/W 3.61, pedipalp chela L/W 8.22, pedipalp manus W/carapace L 0.26, movable finger L/ chela manus ventral L 3.64, pectine teeth 51/49, fixed finger primary denticles 170/171, and movable finger primary denticles 186/180. Vachon (1979) illustrated a specimen from Al Khardj, southeast of Riyadh, another intermediate locality. In Vachon's fig. 5, the pedipalps appear very slender and fall well within our observed range of variation of *A. pterygocercus*. Thus there is no evidence for clinal variation that might bridge morphometric differences between the two species and lead us to synonymize them.

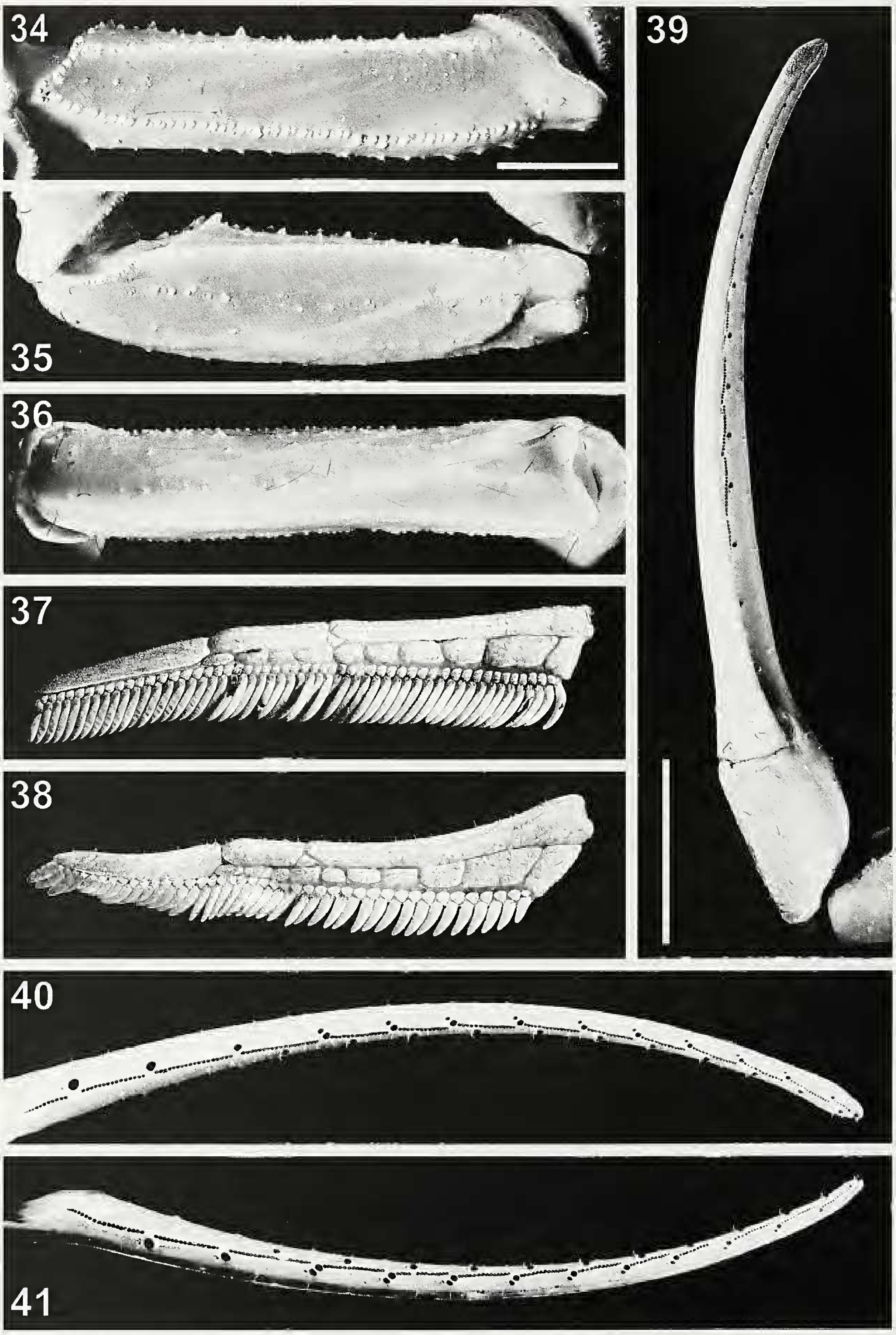
Habitat.—As reported by Navidpour et al. (2008), *A. susanae* collection sites in Khoozestan were restricted to hot, sandy desert at elevations < 35 m (Figs. 28, 29). These sites, along with the record from Kuwait, are situated on a broad alluvial fan around the Tigris-Euphrates River delta (Fig. 27). The substrate consists of sandy soils stabilized by vegetation with low sand hills and nabkha dunes suitable for arenicolous fauna. The habitat of *A. susanae* contrasts with the tall aeolian dunes of Rub' al-Khali, the domain of *A. pterygocercus*. Thomas (1931) vividly portrayed the terrain he encountered at the type locality of *A. pterygocercus*:

> "Uruq Dhahiya, a great immensity of dune country. Vast ridges rise to towering heights; about them are precipitous gorges. It is almost impassable. Again and again we were driven to dismount and to scoop footholds with our hands in the soft yielding slope, so that our camels could climb."

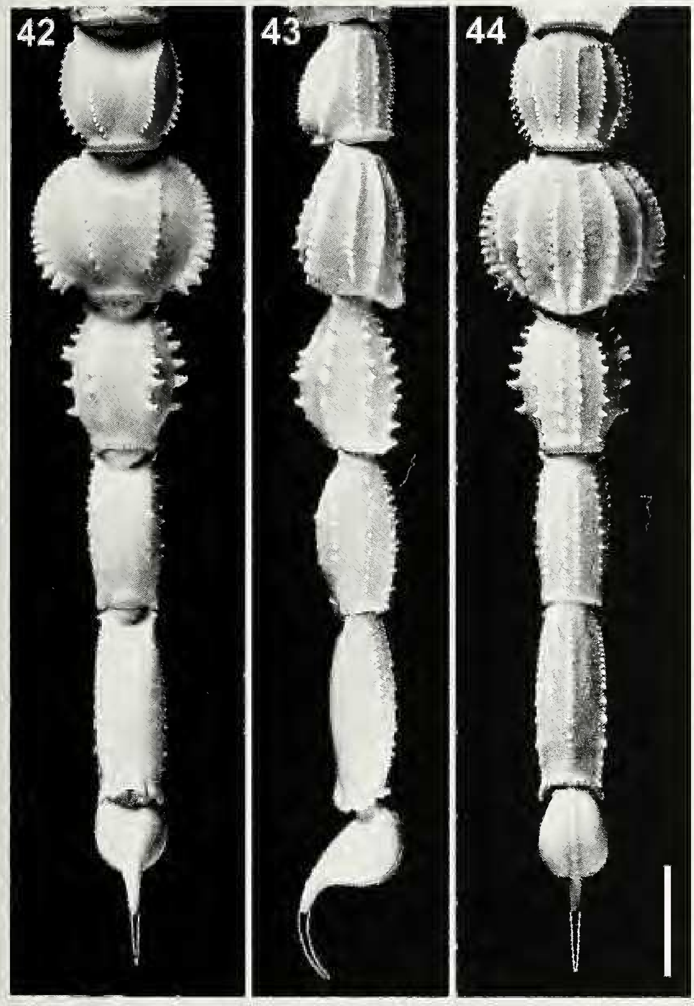
Both species of *Apistobuthus* fit the psammophilous ecomorphotype (Polis 1990; Fet et al. 1998; Prendini 2001a), with long legs and compressed tarsi bearing bristle-combs. Some of the distinguishing features of *A. pterygocercus* may be ultrapsammophilous specializations that evolved to cope with life in less compact wind-blown sands. The longer legs and ungues would enhance traction on soft sand, and also increase the baseline for Rayleigh wave triangulation of prey (Brownell 1977). The latter effect, together with the longer pedipalp fingers, is likely to increase the chances of capturing more sparsely distributed prey in austere dune environments. The adaptive significance of other traits, such as longer pectines, reduced carination, more enlarged metasoma II, and degenerated tibial spurs is unclear. It was speculated that the flared metasoma II with heavily sclerotized lateral and ventral carinae, and the array of sharp spiniform granules on metasoma III, could shield *Apistobuthus* from rear attack by predators while inside a burrow (Lowe 1993). The use of part of the body as a protective barrier inside a burrow is termed "phragmosis," a well known example of which is the function of the disc-shaped abdomen in the trapdoor spider genus *Cyclocosmia* Ausserer 1871 (Gertsch & Wallace 1936; Gertsch & Platnick 1975; Hunt 1976).



Figures 30–33.—*Apistobuthus pterygocercus*, habitus. 30, 31. Adult male from Uruq al Hadd; 30. Dorsal aspect; 31. Ventral aspect; 32, 33. Adult female from 55 km NW Ibri; 32. Dorsal aspect; 33. Ventral aspect. Scale bar = 20 mm.



Figures 34–41.—*Apistobuthus pterygocercus*. 34. Pedipalp femur, dorsal aspect; 35. Pedipalp patella, dorsal aspect; 36. Pedipalp patella, external aspect; 37. Right pectine, adult male; 38. Right pectine, adult female; 39. Pedipalp chela, ventral aspect; 40, 41. Pedipalp chela dentition; 40. Movable finger; 41. Fixed finger. Figs. 34–37, 39: adult male from Uruq al Hadd; Figs. 40, 41: adult male from Wadi Atiyah; Fig. 38: adult female from Margandid. Horizontal scale bar = 2.5 mm in 34, 2.9 mm in 35 & 36, 3.8 mm in 37, 2.4 mm in 38. Vertical scale bar = 5.5 mm in 39, 3.7 mm in 40, 4 mm in 41.

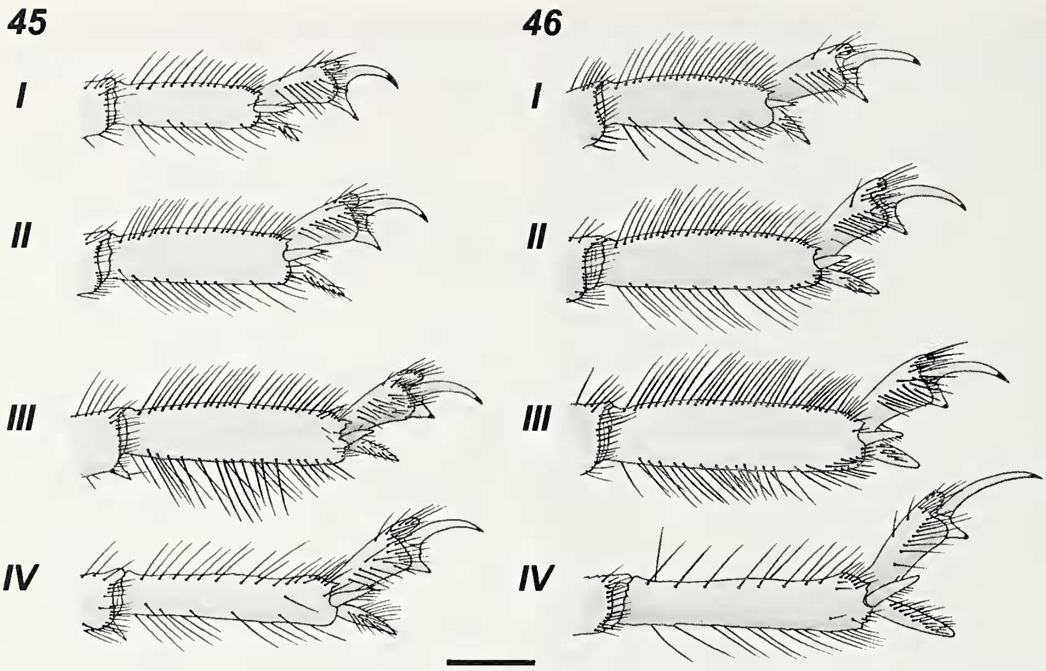


Figures 42–44.—*Apistobuthus pterygocercus*, metasoma, adult male from Uruq al Hadd. 42. Dorsal aspect; 43. Right lateral aspect; 44. Ventral aspect. Scale bar = 7 mm.

Distribution.—The species is known only from Khoozestan Province in South-western Iran, and Kuwait.

Remarks.—Lourenço (1998) correctly recognized the single type specimen from Ahvaz as belonging to a new species of *Apistobuthus*, and he cited four characters that he believed could differentiate it from *A. pterygocercus*. We have analyzed each of these based on larger sample sizes, and we conclude that they cannot serve as reliable diagnostic characters. (1) *Trichobothrial pattern*: the holotype of *A. susanae* was cited as being neobothriotaxic, with trichobothria d_2 and *est* absent on the pedipalp patella. We found that d_2 was small but certainly present on 40/40 pedipalp patellae (n = 20 adults) of *A. susanae* (and present on 62/62 patella from n = 31 adult *A. pterygocercus*). The areolar socket and seta of d_2 were clearly visible under ultraviolet fluorescence microscopy, but were more difficult to resolve under reflected light microscopy and this may have led to erroneous reports of the loss of this petite trichobothrium. In *A. susanae*, 38/40 pedipalp patellae (n = 20 adults) were orthobothriotaxic, bearing all 7 external trichobothria. There were 2/40 cases of trichobothrial loss (n = 2 adults): one patella with *est* lost (unilaterally, right patella), and one patella with esb_1 and esb_2 lost (also right patella). Thus, neobothriotaxy in *A. susanae* is a teratological condition, not representative of the population. We note that *A. pterygocercus* patellae are also normally orthobothriotaxic (59/62 patellae with 7 external trichobothria). (2) *Anal arc dentition*: the holotype of *A. susanae* has 10 teeth on the ventral anal arc, and *A. pterygocercus* was cited as having only 4 teeth. We analyzed the number of major teeth on the ventral anal arc, not including the lateral anal lobe and excluding small denticles that sometimes occurred between the larger major denticles. The number of teeth for *A. susanae* was: 8.20 ± 1.36, range 6–12 (n = 20); for *A. pterygocercus* it was: 8.16 ± 1.44, range 5–11 (n = 31). There was no significant difference in number of anal arc teeth between the two species (U = 293.5, P = 0.75, Mann-Whitney test). (3) *Pectinal tooth count*: the holotype female of *A. susanae* has 29 and 30 pectine teeth, lower than the range of 36–38 cited by Lourenço for females of *A. pterygocercus*. Analysis of our samples shows that *A. pterygocercus* does indeed exhibit higher average numbers of pectine teeth in both sexes (Table 1). However, in our samples the ranges of pectinal tooth counts of females of the two species overlap: 35 is the upper count for *A. susanae*, 32 the lower count for *A. pterygocercus*. Hence, this character is insufficient to diagnose and differentiate the species. (4) *Primary denticle subrows*: the number of subrows on the pedipalp chela fingers was cited as 12 for *A. susanae* versus 14 for *A. pterygocercus*. This characterization does not take into account the fact that in *Apistobuthus* there is a significant difference in the number of subrows for fixed and movable fingers. In a sample of n = 20 adults of *A. susanae*: 37 intact fixed fingers included 32/37 with 13, 2/37 with 12, 2/37 with 11, and 1/37 with 9 subrows; 37 intact movable fingers included 33/37 with 14, 3/37 with 13, and 1/37 with 8 subrows. In a sample of n = 31 adults of *A. pterygocercus*: 60 intact fixed fingers included 3/60 with 14, 53/60 with 13, 2/60 with 12, 1/60 with 11 and 1/60 with 9 subrows; 61 intact movable fingers included 1/61 with 15, 52/61 with 14, 3/61 with 13, 1/61 with 12, 2/61 with 10, 1/61 with 8 and 1/61 with 7 subrows. Thus, excluding a minority of cases involving subrow fusions associated with teratology or finger regeneration after injury, the normal subrow counts are 13 fixed and 14 movable for both species. There was no statistical difference between subrow counts in samples taken from the two species, either for fixed (U = 985.5, P = 0.36) or movable fingers (U = 1114, P = 0.92) (Mann-Whitney test).

On the type specimen of *A. susanae*, Lourenço (1998) noted that petite trichobothrium d_2 on the femur was "very small and placed almost on the internal surface," and actually depicts d_2 on the internal side of the dorsointernal carina (in his fig. 12). We invariably observed a very small seta at the expected location of d_2, and it could be identified as a petite trichobothrium only by having a slightly larger areola compared to the series of presumably chemotactic microsetae deployed along the dorsointernal carina. This presumed d_2 was always clearly positioned on the dorsal surface of the femur, adjacent to granules of the dorsointernal carina, and never on the internal surface. Lourenço (1998) also stated that the β-configuration (Vachon 1975) of femoral trichobothria in the *A. susanae* type specimen was "somewhat atypical" in the genus *Apistobuthus*. We found a β-configuration in all specimens examined of both *A. susanae* and *A. pterygocercus*. Together with the position of patellar d_3, this confirms



Figures 45, 46.—Legs I–IV basitarsus and telotarsus, retrolateral aspect. 45. *Apistobuthus susanae*, adult male from Albaji; 46. *Apistobuthus pterygocercus*, adult male from Wadi Atiyah. Scale bar = 2 mm.

placement of *Apistobuthus* in the "Buthus" group of Fet et al. 2005.

The presence or absence of tibial spurs on legs III–IV is a character with taxonomic value at the genus level (Sissom 1990), and the secondary reduction or loss of tibial spurs occurs in a number of psammophilous scorpions (Fet et al. 2001). We analyzed this character in *Apistobuthus*, scoring a "loss" if the tibial spur was either absent or degenerated to a very small vestigial spur (< 20% the length of a fully developed spur). We found that tibial spur degeneration or loss was infrequent in *A. susanae*, but occurred often in *A. pterygocercus*. In a sample of $n = 20$ adults of *A. susanae*: 39 intact leg III tibia included 30/39 spurs present, 9/39 (23%) spurs lost; 38 intact leg IV tibiae included 34/38 spurs present, 4/39 (10%) spurs lost. In contrast, in a sample of $n = 31$ adults of *A. pterygocercus*: 60 intact leg III tibiae included 15/60 spurs present, 45/60 (75%) spurs lost; 60 intact leg IV tibiae included 36/60 spurs present, 24/60 (40%) spurs lost. The much higher frequency of degeneration or loss of tibial spurs in *A. pterygocercus* correlates to the ultrapsammophile habit of this species, and we suggest that it represents a derived character state.

DISCUSSION

Of the two species of *Apistobuthus*, *A. susanae* appears to be the more plesiomorphic, with shorter, more robust pedipalps and legs, and shorter ungues. These features make it better adapted for a fossorial existence on more stable, compacted sandy soils around the Tigris-Euphrates River delta. Contrasting features of *A. pterygocercus* appear to be apomorphic conditions, some of them associated with life on shifting sands of the Rub' al-Khali. Ancestral *Apistobuthus* scorpions might antedate formation of the Rub' al-Khali. They could have originally evolved on soft alluvial soils of the Tigris-Euphrates drainage, possibly sharing a common ancestor with the fossorial genus *Odontobuthus* Vachon 1950 (Vachon 1960). Genesis of the Rub' al-Khali dunes is thought to be linked to late Pleistocene (< 800 ka BP) high–latitude glaciations that caused reductions in sea level, exposing marine sediments to deflation by strong winds. During these periods of aridity, the Persian Gulf separating Iran from Arabia was dry, and northern trade winds (Shamal), intensified by temperature gradients and high-pressure cells, drove the formation of extensive dune systems on the Arabian peninsula (Glennie 1996). Active dune formation may have also proceeded during less windy, wetter interglacial periods, with local erosion of mountains yielding alluvial deposits that provided additional sources of sand. The complex, extended chronology of the Rub' al-Khali dunes would have provided many opportunities for adaptive radiation of *Apistobuthus* into sands of the Arabian Peninsula, but it is unclear when this occurred. The most recent time window may have been during the last glacial maximum (~ 20 ka BP) when a dune-adapted *A. pterygocercus* could have been derived by rapid stenotopic speciation (Prendini 2001a) from a fluvial-adapted population residing along a Tigris-Euphrates River that flowed through a dry Gulf out to the Strait of Hormuz. Subsequent post-glacial marine transgression of the Persian Gulf would have exerted an isolating influence that accelerated speciation of the ultrapsammophilous species.

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